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THE DEVELOPMENT OF GREGARINES AND THEIR
RELATION TO THE HOST TISSUES: (II) IN
CEPHALOIDOPHORA DELPHINIA (WATSON)*

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This paper is the second of a series in which the writer aims to depict the consecutive stages through which gregarines of various genera pass in becoming mature sporonts, and the relation, whether deleterious or not, which the parasite bears to the intestinal epithelium from which it receives its nourishment. The former paper (Kamm, 1917) contained a brief historical survey of previous investigations of a similar nature.

The parasite chosen in the present instance is *Cephaloidophora delphinia* (Watson), first described by the writer in 1916, the host being the large white beach flea, *Talorchestia longicornis* (Say), taken at Cold Spring Harbor, Long Island, in the summer of 1915. The alimentary tract was removed intact, fixed and preserved. Sections were cut at 4μ and stained with Delafield's hematoxylin. Parasitism was found to occur in more than 30 per cent. of the 260 intestines examined for live sporonts (Watson, 1916); even where gregarines are present, it is rare to find more than a dozen sporonts, and very few intracellular stages in a single host. It is almost by accident that a good infection is encountered.

The alimentary tract of the Gammaridea, a suborder of the Arthropoda, consists (Calman, 1909) of the stomodeum, a long mid-intestine, and a short proctodeum. In my preserved material, most of the stomodeum is missing, having been severed with the head of the flea. At the junction of stomodeum and mid-intestine in *Talorchestia* (Fig. 1) is found one pair of hepatic caeca longer than the rest of the alimentary tract and opening into the same by two ducts. At the union of mid-intestine and proctodeum occurs one pair of caeca opening into the alimentary tract by separate ducts. These caeca are about two-thirds the length of the mid-intestine, looped upon themselves, and finally extend down the proctodeum loosely attached at its side. How they open to the exterior is not determined, as the intestines were clipped off at the posterior end. The caeca are probably excretory in function; they are filled with calcareous concretions for hastening the hardening of the exoskeleton after moults. The proctodeum in *Talorchestia* is nearly as long as the mid-intestine. The former is much thinner-walled than the latter. From the intestinal content one

* Contributions from the Zoological Laboratory of the University of Illinois, No. 123.

sees that the flea feeds upon algae and decaying wood and insects, and it probably finds additional organic matter in dead crabs and fish.

The epithelial cells of the mid-intestine are thrown into fan-shaped lobes (Fig. 6); the individual cells are columnar and packed closely together, and are heavily ciliated on their free surfaces. They are rich in protoplasm, which is either fairly evenly distributed and lightly reticulate or abundant only in the coelomic portion, that part nearer the lumen often being vacuolated. In the proctodeum, where absorption is diminished, the cells are short and broad, more nearly cubical in shape, and the protoplasm is coarsely reticulate. A spiny chitinous lining is present here.

It is in the mid-intestine only that the young parasites find their temporary lodging place. Obviously, the mature free sporonts find conditions at an optimum in the same region where the absorption of chyle is at its maximum. Where sections reveal the presence of sporonts in the lower regions, it is probable that the parasites are being swept down on the periphery of compact food-masses, and are on their way to speedy destruction as the feces are formed and ejected. The mature sporonts, then, collect between the food-masses and the lumen of the mid-intestine for protection, and here also they are in the richest food belt (Fig. 9).

It is a noteworthy fact that no parasites have been found in the hepatic caeca, for in several species studied from insects parasites are found here almost as freely as in the intestine itself. No parasites were found outside the coelomic layer of the epithelium or boring their way through this layer, as was noted in *Stenophora lactaria* (Watson, 1916). Gametes taken from immature developing cysts do not differ in size, but there is a slight difference in staining reaction, indicating a possible sexual differentiation (Watson, 1916). Spores have not been seen to date, neither has the sporozoite been found, and therefore the first stage in intracellular development cannot be shown. Gregarines in all stages of development stain perfectly homogeneously, and for this reason are easily distinguished from surrounding tissue, even in very young stages.

The first stage seen in my sections (Fig. 2) indicates a tiny ovoidal unilocular intracellular parasite smaller than a normal cell-nucleus and situated near the base of the cell which has been penetrated. The trophozoite has begun to absorb nourishment from the cell, which is already vacuolated in the region of the parasite and the nucleus, being nearby, has already begun to shrivel from absorption and probably also from the effect of the parasite excretions. The cell shows no hypertrophy in this early stage.

In a slightly later but still septumless stage of development (Fig. 3) there is also no evidence of hypertrophy, but the originally parasitized cell and the two contiguous ones now show distinct signs of degeneration, the walls in the proximity of the parasite being less clearly defined and the protoplasm more vacuolate than in other parts of the cells. The nuclei have changed from ovoidal to irregularly dolioform in shape.

Figure 4 shows sections of somewhat later stages with more advanced changes in the destruction of the host cells. Where still remaining, nuclei of destroyed cells have shrivelled and stain very darkly, the chromatin granules only being left, and the outlines of the cells have become indistinct throughout.

The next stage (Fig. 5) is that of a small parasite in which a septum is formed dividing it into protomerite and deutomerite. These two parts already show slightly different staining reactions, the former, although containing fewer protoplasmic granules taking the color more readily, a feature characteristic of the parasite throughout the remainder of its life. A small papilla is now visible at the apex of the protomerite which is retained in the adult. Léger and Duboscq (1911) mention this as a "rudimentary structure" and Mercier (1912) calls it an epimerite. It is homologous with a similar structure in *Stenophora lactaria* (Kamm, 1917:126), and both are obviously functionless. As stated for the one previously described, this structure is probably the vestige of an organ which was useful and functional in the past; and this theory would lead to the conclusion that gregarines without or with only vestigial epimerites represent a higher stage of development than forms with a true functional epimerite in the cephalont stage.

Numerous instances have been found in which the parasite has located itself at the base of a lobular group of cells, and in growing is absorbing nourishment from the whole group at once—an arrangement highly advantageous to the parasite, but very destructive to the host tissues. In Figure 6 is shown (*a*) the cross-section of a small gregarine so located. The outline of that portion of the cells nearest the parasite is lost, but parts nearer the lumen still retain much of their individuality. The nuclei in the latter region are still but little affected, but if the nucleus happens to be situated near the parasite it is affected and soon becomes absorbed completely. This proves that nuclei in general are not more susceptible to the presence of the parasite than is the vegetative protoplasm of the cell. The cell-wall next the lumen and the ciliary boundary are the last to lose their identity and often when the entire cell-content has disappeared there is still considerable of the lobular contour left (Fig. 7). No hyper-

trophy is present, the apparent enlargement of the tissue in which the parasite is located being merely the normal contour of the lobules. Thus it is seen that the cells affected by the parasite do not become hypertrophied at any stage, but from the first are absorbed. Therefore, it is apparent that excretions of the gregarine do not seriously affect the cell protoplasm.

Léger and Duboscq (1911) speak of development at first as intracellular and later as intercellular; I should, however, scarcely call the position of parasites of this particular species, after many cells have been totally or partially destroyed, as intercellular.

That the gregarine may occupy any position within the epithelium is indicated in Figure 6, as at *a* it lies horizontal with the basal muscular layer and parallel with relation to the anterior-posterior direction of the intestine; in *b* it lies obliquely; in *c* it lies at right-angles to the long axis of both the intestine and the epithelial cells and in Figure 7 it is seen to lie perpendicular to the long axis of the intestine and parallel to the long axis of the cells. Mercier (1911) mentions that in *Cephaloidophora talitri* the position of the parasite within the cell is not constant. This diversity of position is quite in contrast to that in *Stenophora lactaria*, in which the parasite in almost every instance lay with the protomerite toward the muscular layer at all stages of its development (Kamm, 1917: 126). The explanation for this difference between the two species probably lies in the fact that in *S. lactaria* the parasite is crowded and has no room for movement, while in *C. delphinia* it has considerable freedom for rotation. In its growth *S. lactaria* rarely uses up more than a few cells, while *C. delphinia*, lying at the base of a whole group, uses protoplasm from all and thus gradually vacuolates a large space in which it is more and more free to move. Thus a moderate infection with *C. delphinia* is more destructive to its flea host than is a similar infection of *S. lactaria* to its milliped host.

After the whole parasitized space has been vacuolated and the nourishment has been exhausted, and when the walls next the lumen along with their ciliary boundary have disintegrated (Fig. 8), the parasite is free to give up its confinement and becomes free-living within the lumen of the canal. It is quite probable that the limiting wall is often violently ruptured by the increasingly active movements of the animal.

After the parasite has liberated itself and migrated into the lumen, it becomes a sporont. This departure is entirely due to accident, the parasite in its movements finding the opening which has been made into the lumen. The mode of assimilation of the sporont undergoes little change from that of the trophozoite; instead of receiving its

nourishment from the cell, food is absorbed before it is taken up by the cell. The animal leads a more or less sluggish life even when freed, for groups are found lying close to the cilia and embedded in mucous masses (Fig. 9; see also Watson, 1916, Fig. 3). Mature live sporonts measure approximately 110μ by 60μ .

After the cell-group is rid of its exhausting burden, it is practically destroyed; there is little protoplasm left and no nuclei to recover from the shock and with which to reconstruct the shattered group. Certain small barren areas are sometimes seen in cross-sections of the epithelium, and these structureless regions may be caused by destruction due to parasites. There are two other possibilities, however, concerning the vacated cells: The surrounding unaffected cells may gradually enlarge and close entirely over the space, or regeneration of the destroyed tissue may take place.

In instances of maximum infection noted, the effect of parasitism upon the host is undoubtedly deleterious. When twenty or more cells are completely destroyed by each parasite of a hundred or more developing at the same time, the absorptive capacity of the intestine is greatly diminished. I was, however, unable to prophesy from the action of live fleas which would be the more prolific in parasites, tho this had been done in the case of some hosts parasitized with enormous numbers of gregarines, or nematodes, or both (e. g., various grasshoppers and *Diabrotica vittata*, the cucumber beetle).

The parasite does not attain its maximum growth within the epithelium but grows considerably after becoming free (contrast Figs. 8 and 10). During its sporont life it becomes attached to another of its kind and ultimately the two conjoints form a cyst. This process has already been described for the species in question (Watson, 1916:131).

Three species were described by the writer in 1916 as *Frenzelina delphinia*, *F. olivia* and *F. nigrofusca* from beach fleas, fiddler crabs and littoral spider crabs. I find in a footnote in an article by Léger and Duboscq (1911) that the genus name *Frenzelina* Léger and Duboscq (1907) is preoccupied by a rhizopod, *Frenzelina* Penard 1902; and that the genus name for the gregarine becomes *Cephaloidophora*, given by Mawrodiadi in 1908. Therefore my three species become, respectively, *Cephaloidophora delphina*, *C. olivia* and *C. nigrofusca*.

SUMMARY

Consecutive stages in the growth of *Cephaloidophora delphinia* (Watson) are shown.

This species does not possess an epimerite.

Development is intracellular.

Many cells contribute to the nourishment of the parasite, all of which are ultimately destroyed.

No noticeable hypertrophy of either nucleus or vegetative protoplasm of the host cells is indicated.

Large infections are deleterious to the host.

REFERENCES CITED

- Calman, W. T. 1909.—Lankester's Treatise on Zoology, pt. VII, Appendiculata; fas. 3, Crustacea; 346 pp.
- Kamm, Minnie Watson. 1917.—The Development of Gregarines and Their Relation to the Host Tissues: (I) in *Stenophora lactaria* Watson. Jour. Parasit., 3: 124-30.
- Léger, L., and Duboscq, O. 1911.—Deux Grégarines de Crustacés. *Porospora portunidarum* Frenz. et *Cephaloidophora maculata* n. sp. Arch. zool. expér. et gen., (5) 6: lix-lxx; 6 figs.
- Mercier, L. 1912.—*Cephaloidophora talitri* n. sp. Grégarine parasite du Talitre. C. R. soc. biol., 72: 38-39; 1 fig.
- Watson, Minnie E. 1916.—Three New Gregarines from Marine Crustacea. Jour. Parasit., 2: 129-36; 1 pl.

EXPLANATION OF PLATE

The reference line is 0.03 mm. long.

Fig. 1.—Alimentary tract of *Talorchestia longicornis* (Say), from preserved material, *h c*, hepatic caeca; *m i*, mid-intestine; *e c*, excretory caeca; *p* proctodeum.

Fig. 2.—Early stage in growth of trophozoite, septumless, host cell-nucleus already affected.

Fig. 3.—Later stage, similar to last, contiguous cells being vacuolated.

Fig. 4.—Two cross-sections of young trophozoites, showing marked influence upon the epithelium.

Fig. 5.—Half-grown trophozoite with septum formed.

Fig. 6.—Parasites in three situations within host-tissue; (*a*) cross-section, position most favorable for absorbing nourishment from many cells; (*b*) oblique position, with marked destruction of tissue; (*c*) longitudinal section of nearly full-grown trophozoite.

Fig. 7.—Third position of parasite, parallel to long axis of the cells. Cell wall toward lumen weakened.

Fig. 8.—Cell wall broken preparatory to trophozoite migration.

Fig. 9.—Sporonts in lumen of upper proctodeum.

Fig. 10.—Mature associated sporonts, free in upper portion of proctodeum. Glycerine mount.

KAMM—DEVELOPMENT OF GREGARINES. II

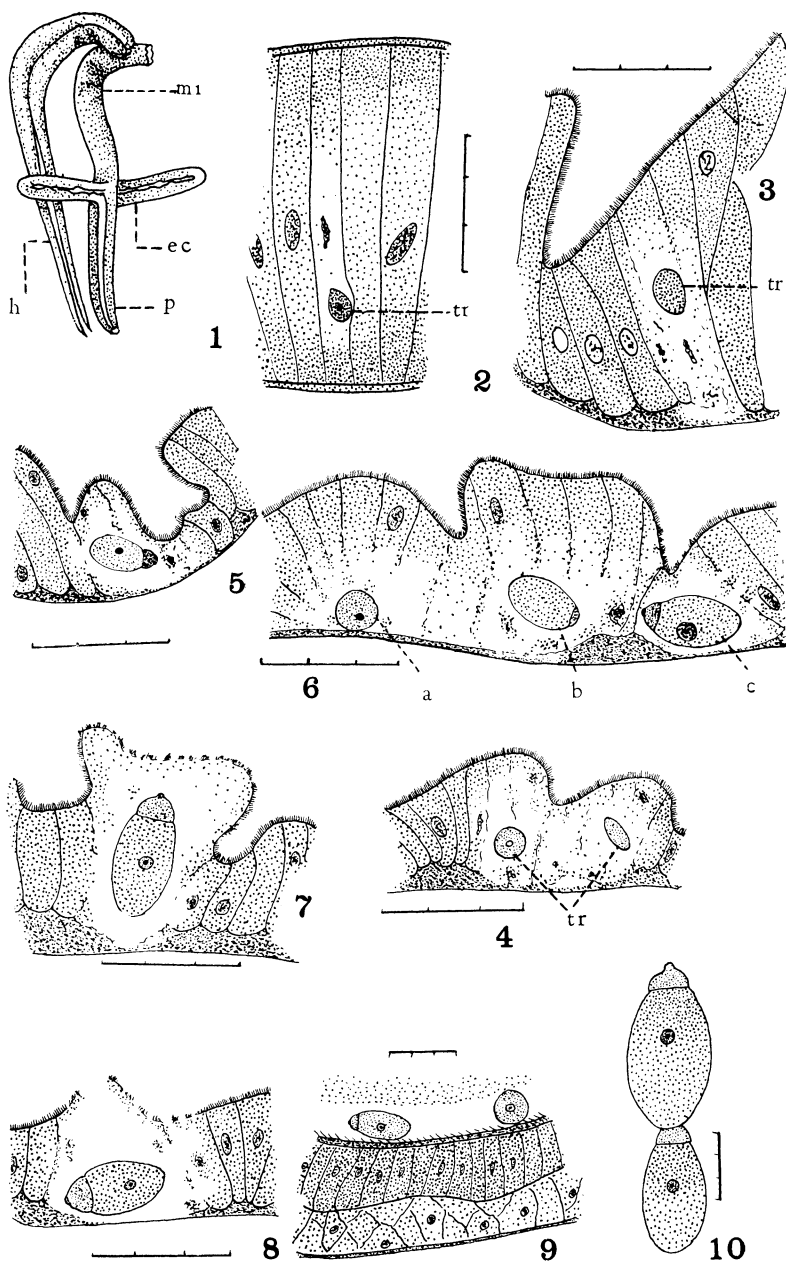


PLATE IV